

ABSTRACT

I studied the ecology, behavior, and demography of the noncooperatively breeding Western Scrub-Jay (*Aphelocoma californica californica*) in central coastal California. Cooperative breeding is ancestral in *Aphelocoma* jays and its loss in Western Scrub-Jays presents an opportunity for appropriate phylogenetic and ecological comparisons within the genus to identify key factors selecting for the alternative social systems. My intent was to gather comparative data to test several models for the evolution and maintenance of delayed dispersal and group living in birds, which were developed from long-term studies of cooperative breeders, including the closely related Florida Scrub-Jay (*A. coerulescens*) and Mexican Jay (*A. ultramarina*). The fundamental result of these comparisons is that models for the evolution of delayed dispersal and group living in birds fail as general explanations when floating is ignored or treated as a one-dimensional phenomenon. Factors that lead to delayed dispersal in cooperative species are known to be complex and may differ substantially among species and populations, and even among individuals within populations and groups. Conditions leading to early dispersal and floating may be equally complex. Clearly, opportunities for independent breeding are constrained in both cooperative and noncooperative populations. What then makes early dispersal and floating the preferred strategy in Western Scrub-Jays? Several factors play a part, including (1) the interplay between the pattern of habitat quality and acorn production, (2) the varied behaviors floaters may employ to exploit these resources and acquire breeding space, (3) the behavioral interactions between territorial jays and floaters, and (4) the ability of floaters to settle on low-quality territories and then, as breeders, to move and improve the quality of their territories.

California Scrub-Jays are monogamous, permanently territorial, and noncooperative breeders. Offspring depart from their natal territories at independence, yet breeders tolerate both offspring and unrelated floaters of all ages on their territories except during May and June. Because of this tolerance, juveniles and older floaters aggregate in the highest quality habitats on occupied territories, primarily where acorns are in good supply. Although floaters exhibit diverse dispersal behavior, most remain sedentary throughout the winter and early spring, storing and recovering acorns as do the resident territorial breeders. By late April in most years, the aggregations dissolve and floaters are rarely seen until some of these same individuals return in early July and join large numbers of independent juveniles. The disappearance of floaters is coincidental with increased aggression by territorial jays, but floaters also disappear from areas not occupied by breeders.

Floating in scrub-jays took several forms. Some banded juveniles remained on and around their natal territories until the next breeding season, others joined aggregations a short distance away or disappeared. In four of five years, the study area attracted floaters from a wide area. In the anomalous year (when the acorn crop failed), local juveniles departed and no floaters immigrated. In winter, floaters occasionally established pseudo-territories that were abandoned in the late spring. Other floaters moved widely (up to 35 km) during the winter, but the majority established defined home-ranges from fall to early spring. In April of one year, large flocks of up to 60 jays in transit were observed. The few floaters seen during May and June in most years were individually sneaking through territories or, more rarely, moving in unoccupied habitat. In one year (1985) of high acorn abundance lasting until April, floaters remained on their home ranges (which overlapped an average of nine territories) throughout the breeding season; this was coupled with increased tolerance by breeders.

Breeder survivorship averaged 83% and 79% per year for males and females, respectively, and reproductive output averaged 1.4 fledglings per pair. Reproductive success of jays that acquired territories as yearlings was near zero and did not peak until age four.

Over the five-year period and 215 pair-years, first-year males and females comprised 5% and 10%, respectively, of the breeding population. Of 12 jays that both fledged from and later acquired territories on the study area, five did so as yearlings, four as two-year olds, and three as three-year olds. Nearly all jays gained a territory by pairing with an older, established breeder. Life-table estimates, based upon these and other demographic data, indicate that 19% and 40% of males and females, respectively, acquire territories as yearlings. An analysis of territorial dynamics, including the types of habitats used, occupancy rates of territories, and vegetation characteristics, suggest that all suitable habitat is occupied by breeders in most years and that ecological constraints prevent a sizeable portion of first-year jays from acquiring territories and breeding.

Individual jays cache approximately 7,000 acorns each year. Poor acorn years result in significantly higher mortality, reproductive failure, and territory abandonment. The 1983 crop failure, through the effects of higher mortality and territory abandonment, resulted in a 25% decrease in the number of territories on the study area and the potential for new breeding vacancies. Acorn production by the large and patchily distributed oaks in California is highly variable locally within and among years, and periodic crop failures occur every 4 to 6 years, depending on the number of oak species in the area.

Early dispersal is favored because floaters are able to aggregate in areas of high acorn abundance, and the

tolerance of floaters by breeders allows them access to the best habitats. Floaters appear to be as dependent on cached acorns as breeders and may be closely tied to these stores during the winter. Floaters may spend fall and winter in areas of high acorn production, despite the fact that these areas provide relatively few breeding opportunities. In the spring, near continuous distribution of oak woodland provides lepidopteran larvae and other insects over a wide area. Floaters are then free to move regionally and search out breeding areas, particularly in areas of prior acorn crop failures that may offer more territory vacancies. This pattern of food abundance may also contribute to the tolerance of floaters in the winter (when acorns are superabundant) and intolerance in the breeding season (when insect prey is important and starvation rates of nestlings are high).

Key words: *Aphelocoma*, acorn production, cooperative breeding, dispersal, floating, scrub-jay, social behavior.

INTRODUCTION

Long-term field studies have contributed greatly to our knowledge of the demographic and ecological factors that promote delayed dispersal, larger group size, and increased cooperation in cooperatively breeding birds. Theories based on these studies differ in stressing the relative importance of various demographic and ecological factors both in the maintenance of cooperative breeding and in modeling the evolution of group living and cooperative breeding from an earlier noncooperative state. Similar long-term studies of appropriate noncooperative species are essential for the comparisons required to test these theories and their underlying assumptions. The Western Scrub-Jay (*Aphelocoma californica*) and other species in the genus provide a unique and unparalleled opportunity to make such comparisons. *Aphelocoma* jays are similar in morphology and general aspects of behavior, their social organization ranges from the noncooperative Western Scrub-Jay to the plural-breeding, cooperative Mexican Jay (*A. ultramarina*), and there is a wealth of information on two cooperative members of the genus, the Mexican Jay and the Florida Scrub-Jay (*A. coerulescens*).

APHELOCOMA JAYS

Nearly all races of scrub-jays in western North America breed noncooperatively. Young disperse from their natal territories soon after becoming independent and then, over the ensuing months, attempt to acquire territories and breeding status. Despite their wide geographic range and the diversity of habitats used, only one population (*A. californica sumichrasti*) in the mountains of southeastern Mexico is known to live in family groups (Burt and Peterson 1993).

The insular Island Scrub-Jay (*Aphelocoma insularis*) has been the best studied western population (Atwood 1980a,b; Atwood et al. 1990); it became isolated from the mainland population during the Pleistocene (Pitelka 1951), almost certainly after the western populations had lost traits of cooperative breeding (see below). In contrast to the noncooperative Western Scrub-Jays, the cooperatively breeding Florida Scrub-Jay (Wolfenden 1974, 1975; Wolfenden and Fitzpatrick 1977, 1978, 1984, 1986, 1990; Fitzpatrick and Wolfenden 1986, 1988; Mumme 1992) and Mexican Jay (Brown 1963, 1970, 1974, 1994; Brown and Brown 1981a, 1984, 1990; Brown et al. 1997; Trail et al. 1981) have been intensively studied for 25+ years. In Florida Scrub-Jays, offspring from a single breeding pair may delay dispersal for one to several years, forego breeding, and help in defending the territory and raising offspring in subsequent breeding efforts. Roughly one-half of all pairs have helpers in any given year. The Mexican Jay exhibits geographic variation in group size and social behavior (Strahl and Brown 1987, Brown and Horvath 1989) ranging from singular breeding (one breeding female per group) to